Response of Barley to Grasshopper Defoliation in Interior Alaska: Dry Matter and Grain Yield

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ABSTRACT   Barley, *Hordeum vulgare* L., is well adapted to subarctic Alaska growing conditions, but little is known about its response to grasshopper defoliation. A field experiment was conducted to study dry matter and grain yield in response to a combination of grasshopper defoliation and weeds in 2002 and 2003 near Delta Junction, AK (63° 55′ N, 145° 20′ W). Barley plants at third to fourth leaf stage were exposed to a combination of two levels of weeds (present or absent) and four densities of grasshoppers (equivalent to 0, 25, 50, and 75 grasshoppers per m^2) of third to fourth instars of *Melanoplus sanguinipes* (F). Dry matter accumulation by the barley plants was determined at three times during the growing seasons: $\approx$10 d after introduction of the grasshoppers, shortly after anthesis, and at maturity. Dry matter accumulation and grain yield were much lower in 2003 than in 2002, probably due to very low levels of soil moisture early in the growing season of 2003. Head clipping accounted for a greater portion of yield loss in 2003 than in 2002. The percentage of reduction in harvestable yield due to grasshoppers remained fairly constant between years (1.9 and 1.4 g per grasshopper per m^2 in 2002 and 2003, respectively) despite a large difference in overall yield. Examination of the yield components suggest that yields were reduced by the early season drought in 2003 primarily through fewer seeds per head, whereas grasshoppers in both years reduced average seed weight, but not numbers of seeds.

KEY WORDS   barley, yield, subarctic, harvest index, sink-limitation

MANY WEEDS AND INSECT pests, such as grasshoppers, are well adapted to habitats created by modern agricultural practices, perhaps in part due to fewer natural enemies and/or competitors present in these habitats (DeBach and Rosen 1991, Pfadt 1994, Patterson 1995, Swanton and Murphy 1996). In the late 1970s, $\approx$50,000 ha of land in interior Alaska was cleared of native vegetation (primarily forest) for cultivation of small grains and other crops (Lewis and Wooding 1978, Knight and Lewis 1986). Grasshoppers, primarily *Melanoplus sanguinipes* (F.), but also *Melanoplus borealis* (Fieber) and *Camnula pellucida* (Scudder), inflicted heavy losses on cereal crops and vegetables during outbreaks in 1988, 1992, and 1994 in Alaska (Quarberg and Jahns 2002). Over the past 50 yr in Canada and the United States, grasshoppers caused an average annual crop loss of $6 million to cereal crops, with losses as high as $200 million in an outbreak year (Gage and Mukerji 1978, Olfert 1986).

Source–sink relationships of cereal crops during grain fill have been of considerable interest to agronomists for the insights it may provide for breeding programs (Schnyder 1993). Potential yield is set at anthesis and depends on the growth of vegetative structures (source), number of primordia formed during floral initiation, and the number of fertile spikelets at anthesis (sink) (Gallagher et al. 1976, Gardner et al.

1985). Potential yield may be limited by poor growing conditions during vegetative growth stages, when competition for assimilates among the different plant organs may limit the number of fertile spikelets formed or pollinated (Rackham 1972, Gallagher et al. 1976, Asseng and van Herwaarden 2003). Actual, or realized, yield is determined postanthesis during grain filling. When postanthesis growing conditions are good, the demand for carbohydrates by the developing grains can be met primarily by current photosynthesis (Schnyder 1993, Wardlow and Willenbrink 1994). Grain yields may be buffered against postanthesis drought, defoliation, and other stresses by remobilization and translocation of preanthesis assimilates to the grains (Schnyder 1993, Wardlow and Willenbrink 1994, Asseng and van Herwaarden 2003). Borras et al. (2004) have suggested that yields of spring wheat are most commonly limited by the ability of the developing grains to take up assimilates, i.e., sink limitation. Source limitation has been demonstrated in barley stressed by late-season drought (Voltas et al. 1997, 1998).

Barley is one of the few small grains that is well adapted to the short growing season of the subarctic. Grasshopper feeding may result in season-long, chronic defoliation when newly hatched grasshoppers invade the crop from adjacent heavily infested areas

(such as rangeland or roadside) or when crops are seeded in infested stubble (Pickford and Mukerji 1974, Pfadt 1994), common occurrences in Alaska. Later in the season, generally postanthesis, adult grasshoppers may fly some distance to invade crops. By consuming photosynthetic tissue, grasshoppers limit vegetative growth during preanthesis and limit the amount of assimilate available to the developing grain during postanthesis. Late in the season, grasshoppers also may reduce the number of harvestable heads by damaging the peduncle (head clipping), resulting in either dropped or hanging heads that are unharvestable.

Several studies have investigated the relationship between grasshopper density, damage, plant growth, and yield loss in field crops (Pickford and Mukerji 1974, Capinera and Roltsch 1980, Olfert and Mukerji 1983, Wright 1986, Olfert and Slinkard 1999). In studies of defoliation (either by insects or leaf clipping) of cereal crops, the most common treatment is a one-time acute defoliation (Ryle and Powell 1975, Mukerji et al. 1976, Olfert and Mukerji 1983, Sharrow 1990, Begna and Fielding 2003). One-time defoliation may mimic the effects of a sudden influx of adults, or hatching of high-density populations at the field margins, which are then chemically controlled. A more typical situation may be chronic defoliation occurring over time, such as when crops are seeded in infested stubble or there is a steady migration into the crop. Also, grasshopper damage usually occurs in combination with weeds or diseases, but very few studies include the combined effects of weeds or diseases and grasshoppers. Thus, the objective of this study was to quantify the effects of grasshopper herbivory and weeds on dry matter accumulation and yield components of barley under subarctic conditions.

Materials and Methods

Barley dry matter and grain yield response to a combination of weeds and grasshopper defoliation were studied in 2002 and 2003 at Delta Junction, AK (63° 55′ N, 145° 20′ W). The soil was a Volkmar silt loam (coarse silty over sandy-skeletal, mixed, superactive Aquic Eutrocryepts). The study was conducted on land that was previously cleared and put into agricultural production, subsequently abandoned, and recently recleared of second-growth trees. Before planting, soil was fertilized (broadcast and incorpo-

rated by disking) with 115 kg N ha^{-1}, 57 kg of P_2O_5, 68 kg of K_2O, and 25 kg S ha^{-1} in both years. The seed (variety Otal, commonly grown in Alaska) was planted at ≈100 kg ha^{-1} on 21 May and 13 in 2002 and 2003, respectively. Weather data for the two growing seasons and long-term averages were obtained from a National Oceanic and Atmospheric Administration weather station located ≈20 km northeast of the study site (NCDC 2004).

Grasshoppers were confined within cages covering an area of 0.25 m^2 and ≈120 cm in height. Cages consisted of a bag made from Econet B insect barrier (LS Americas, Charlotte, NC) supported by bamboo sticks with the bottom of the bags buried in the soil. The mesh was rated as transmitting >85% of direct sunlight and reducing airflow by <5%. Cages were stocked with third to fourth instars of *M. sanguinipes* when barley plants where at the third to fourth leaf stage (on 20 June 2002 and 23 June 2003). Weeds were removed by hand from the weed-free plots during cage setting, whereas the weedy plots (naturally occurring weeds) were left uncontrolled. Generally, weeds were at approximately one- to two-leaf stage (visual observation) at this time. Weeds primarily consisted of common lambsquarters, *Chenopodium album* L.; fireweed, *Epilobium angustifolium* L.; field horsetail, *Equisetum arvense* L.; and corn spurry, *Spergula arvensis* L.

The experiment was organized as a split plot with the plots arranged in a randomized complete block design with four blocks. Weed treatments (weed free and weedy) formed the main plot, whereas grasshopper density formed the subplots. Cages were stocked with four levels of grasshopper density: 0, 9, 18, and 27 per cage, equivalent to 0, 36, 72, and 108 grasshoppers per m^2. Counts of live grasshoppers at the second and third harvests were ≈70% of the initial stocking densities. Each treatment was replicated four times.

In both 2002 and 2003, plants were harvested three times: harvest 1, preanthesis, 10 d after stocking the cages; harvest 2, ≈4 wk after harvest 1, shortly after anthesis; and harvest 3 at maturity. Grasshoppers were at about fourth to fifth instars at the first harvest and in the adult stage during the second and third harvests. At each harvest, plants were cut at ground level and then dried for 72 h at 70°C. Whole-plant aboveground dry matter was recorded for the first two harvests. For the final harvest, intact, clipped (dropped), and hanging heads were harvested separately. Heads were con-

Table 1. Growing degree-days and precipitation (millimeters) during the 2002 and 2003 growing seasons, and 30-yr means (from 1971 to 2000), at NOAA station at Big Delta Allen AAF, AK

Yr	May	June	July	Aug.	Sept.	Total
			Growing degree-days			
2002	152.5	257.2	319.4	206.9	89.2	1025.2
2003	89.2	290.6	320.3	238.3	51.4	989.8
30-yr mean	115.3	271.1	336.4	249.1	68.0	1039.9
			Precipitation (mm)			
2002	12.0	79.5	53.0	87.8	31.5	263.8
2003	7.5	7.8	90.8	42.8	32.8	181.7
30-yr mean	21.4	59.8	71.9	52.4	23.1	228.6

sidered to be hanging only if due to grasshopper damage, based on chewing marks on stems. Heads were threshed and grain yield of intact and dropped or hanging heads was determined separately. Awns and chaff were included in whole aboveground dry matter of the last harvest. In addition to final grain yield, number of seeds per head and 100-seed weight were recorded. Harvest index, the ratio of grain to total aboveground biomass (grain plus aboveground dry matter) also was calculated.

Weeds from the weedy plots (within the cages) were collected at the first two harvests, for biomass in both 2002 and 2003. Weed species were determined at the first harvest for 2002 and at the second for 2003. Total combined biomass of all weed species and the dominant weed species, common lambsquarters, was recorded.

Statistical analyses were performed using the GLM procedure of SAS Institute (1994). Data from the 2 yr were tested for homogeneity of variance and found to be heterogeneous in both years; therefore, variables were subjected to a square-root transformation. The statistical model was based on a split-split plot, with year as the main plot, weed treatments as subplot, and levels of grasshopper density as the sub-subplot. When the F-test was significant ($P < 0.05$), a protected least significance difference (LSD) test was used to detect differences between means. Additionally, regression analysis, with linear and quadratic terms, was performed to determine the relationship between grain yield and levels of grasshopper density.

Results

Crop Establishment. Overall growing conditions, especially moisture availability, were better in 2002 than in 2003. Early season precipitation was far below normal in 2003 (Table 1), but the dry conditions were alleviated in July. In addition, May 2003 was cooler and June 2003 warmer than normal (Table 1). Mean plant density, 286 and 211 per m^2 in 2002 and 2003, respectively, did not differ significantly between years (Table 2).

Aboveground Dry Matter Accumulation. The analysis of variance (ANOVA) showed a significant effect of year on aboveground dry matter accumulation for all harvests (Table 2). The unfavorable early season growing conditions in 2003 were reflected in the large difference in dry matter accumulation between years at the first harvest (Fig. 1). Dry matter accumulation in 2003 was lower than in 2002 by 89, 70, and 55% for harvests 1, 2, and 3, respectively (Fig. 1). These differences in dry matter between years were apparently due to the insufficient soil moisture for early vegetative growth during the 2003 growing season. The loss of nongrain dry matter from anthesis (harvest 2) to maturity (harvest 3) was much greater in 2002 than in 2003 (Fig. 1).

Aboveground dry matter of barley was significantly affected by levels of grasshopper density during all harvests, except the first and second harvests in 2003. Even though crop biomass was lower in 2003, but

Table 2. Results of analysis of variance showing probabilities (and F values) for main and interaction effects of year, weed treatment, and grasshopper density on dry matter and yield related variables

Dependent variable	CV[a]	Factor					
		Year df = 1, 3	Weeds df = 1, 6	Grasshoppers df = 3, 36	Yr*weeds df = 1, 6	Yr*Grasshoppers df = 3, 36	Weeds*grasshoppers df = 3, 36
Intact grain yield	17.8	0.0009 (184.1)	0.9323 (0.4)	<0.0001 (12.1)	0.7905 (0.1)	0.7410 (0.4)	0.1982 (1.6)
Hanging and clipped grain	63.1	0.0552 (9.3)	0.2544 (1.6)	<0.0001 (18.7)	0.3565 (1.0)	0.0022 (5.9)	0.7955 (0.3)
All grain[b]	18.3	0.0020 (103.2)	0.5485 (0.4)	0.0016 (6.2)	0.5872 (0.3)	0.9594 (0.1)	0.2553 (1.4)
Seeds per head	11.2	0.0154 (25.0)	0.3040 (1.3)	0.3949 (1.0)	0.0621 (5.2)	0.9284 (0.2)	0.5939 (0.6)
Seed wt[c]	6.0	0.0018 (112.2)	0.4705 (0.6)	<0.0001 (10.8)	0.6468 (0.2)	0.3151 (1.2)	0.4214 (1.0)
Barley plants/m³	14.1	0.1520 (3.7)	0.1503 (2.7)	0.1751 (1.8)	0.5590 (0.4)	0.7416 (0.4)	0.5363 (0.7)
Dry matter[d], first harvest	16.5	0.0006 (230.2)	0.1897 (2.2)	0.0422 (3.0)	0.1391 (2.9)	0.2407 (1.5)	0.2338 (1.5)
Dry matter[d], second harvest	19.6	0.0023 (94.5)	0.2055 (2.0)	0.0401 (3.1)	0.1908 (2.2)	0.4545 (0.9)	0.3604 (1.1)
Dry matter[d], third harvest	15.2	0.0021 (101.4)	0.2036 (2.0)	<0.0001 (11.8)	0.4338 (0.7)	0.2044 (1.6)	0.5326 (0.7)
Harvest index[e]	8.1	0.0047 (57.9)	0.8608 (0.0)	0.3886 (1.0)	0.9169 (0.0)	0.8304 (0.3)	0.2151 (1.6)
Weed dry matter, first harvest	35.9	0.0031 (76.6)		0.0988 (2.4)		0.0548 (3.1)	
Weed dry matter, second harvest	61.4	0.0105 (33.0)		0.5406 (1.0)		0.9202 (0.2)	

[a] CV, coefficient of variation.
[b] Combined weight of grain in intact heads plus clipped and hanging.
[c] Dry weight of 100 seeds.
[d] Aboveground dry matter, excluding grain.
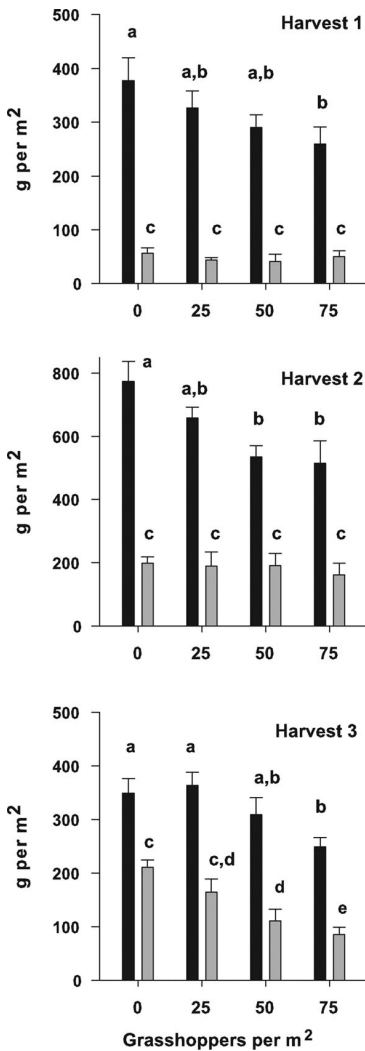[e] Ratio of grain to aboveground dry matter plus grain on dry weight basis.

Fig. 1. Mean aboveground dry matter (excluding grain) of barley at four levels of grasshopper density in 2002 (black bars) and 2003 (gray bars). Means with the same letter do not differ significantly at $P < 0.05$, LSD. Harvest 1 occurred before anthesis; harvest 2, shortly after anthesis; and harvest 3 at crop maturity.
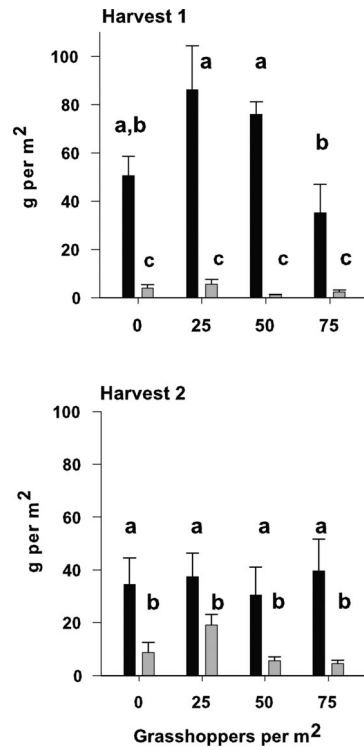

Fig. 2. Mean aboveground dry matter of weeds at four levels of grasshopper density in 2002 (black bars) and 2003 (gray bars). Means with the same letter do not differ significantly at $P < 0.05$, LSD. Harvest times as in Fig. 1.

grasshopper density was similar, grasshoppers had no significant effect on early season accumulation of dry matter in 2003 (Fig. 1).

Presence or absence of weeds had little or no effect on dry matter accumulation, probably due to low weed pressure during both years. In 2002, the total biomass of all weeds combined was 22 and 6% that of the crop biomass at first and second harvests (averaged over levels of grasshopper density), respectively; and in 2003, it was only 6 and 5% at the first and second harvests, respectively (Fig. 2). Common lambsquarters was the dominant weed species, making up 78 and 27% of the total weed biomass in 2002 and 2003, respectively.

Grain Yield and Yield Components. No interaction effects (year × weeds, year × grasshoppers, and weeds × grasshoppers) for grain yield were significant (Table 2). The response of grain yield to the main effects (year, weed, and grasshoppers) was similar to that of dry matter, being affected by year and grasshopper density, but not by weed treatment. Grain yield, averaged over all levels of weed and grasshopper density, was much higher in 2002 than 2003 (Table 3).

Yield loss due to grasshoppers was increased by clipped and/or hanging heads (Table 3). There was an interaction of year × levels of grasshopper density for yield loss through clipping (Table 2). In 2002, yield loss through clipping and hanging heads was not significantly different from zero at the low and medium grasshopper densities, whereas in 2003, all of the three levels of grasshopper density resulted in significant head clipping compared with the control (zero grasshopper) treatment. Head clipping at all levels of grasshopper density was significantly higher in 2003 than in 2002. Grain from clipped or hanging heads represented <2% of total grain production in 2002 but was ≈29% of total grain production in 2003, when averaged over all nonzero levels of grasshopper density.

In both 2002 and 2003, yield decreased with increasing grasshopper density (Table 3; Fig. 3). Quadratic terms were not significant in regressions of yield on grasshopper density in either year ($F = 1.16$; df = 1, 29; $P = 0.29$ and $F = 0.02$; df = 1, 29; $P = 0.98$ for 2002 and 2003, respectively). The percentage of reduction

Table 3.   Mean (SD) grain yield from intact, clipped and hanging, and total heads of barley at Delta Junction, AK, in 2002 and 2003

Yr	Grasshopper density			
	0	25	50	75
2002 Intact	352.8 (95.1)a[a]	350.1 (61.7)a	278.9 (87.7)b	217.6 (61.4)b
Clipped	0.0 (0.0)b	2.4 (3.7)b	3.0 (3.5)b	9.7 (10.1)a
Combined	352.8 (95.1)a	352.5 (62.8)a	282.0 (85.5)b	227.3 (59.7)b
2003 Intact	157.4 (52.8)a	129.9 (95.0)ab	84.9 (48.2)bc	58.2 (41.2)c
Clipped	0.0 (0.0)b	33.3 (23.7)a	42.4 (42.6)a	37.1 (26.1)a
Combined	157.4 (52.8)a	163.1 (111.4)a	127.3 (82.0)ab	95.3 (64.1)b

Yield in grams per square meter and grasshopper density in numbers per square meter.
[a] Means in a row followed by the same letter are not significantly different ($P \leq 0.05$), LSD.

in harvestable yield due to grasshoppers was greater in 2003 than in 2002, primarily because of more head clipping in 2003 (Table 3). The reduction in harvestable yield, averaged over weed treatments, due to grasshopper damage was in the order of high > medium > low grasshopper density (38, 21, and 0.8% and 63, 46, and 17% for 2002 and 2003, respectively) (Table 3). When clipped or hanging heads were included in the yield, grasshoppers reduced total grain production to a similar degree in both years (20 and 36% and 19 and 39% for the medium and highest grasshopper densities in 2002 and 2003, respectively.

ANOVA revealed a strong effect of growing conditions (year) on number of seeds per head and average seed weight (Table 2). When averaged over all levels of weed and grasshopper density, seed number per head was 41% lower and seed weight was 23% higher in 2003 than in 2002 (Fig. 4).

Harvest index was affected only by year (harvest index of 0.48 versus 0.41 in 2002 and 2003, respectively) and not by weed treatment or levels of grasshopper. Harvest index, averaged over all levels of weed treatment and grasshopper density, of the 2003 growing season was 17% lower than the harvest index in 2002, reflecting the different patterns of dry matter and yield in the 2 yr (Fig. 1; Table 3).

Discussion

The lower grain yield in 2003 compared with 2002, averaged over levels of weed treatment and grasshopper density, was probably due to early season weather conditions. Drought is one of the main abiotic factors that severely affects agricultural systems and food production throughout the world (Boyer 1982). Even intermittent water stress, especially at critical stages of crop development, has been reported to reduce dry matter production and grain yield (Ludlow and Muchow 1990, Sharratt 1994). Reduction in dry matter and yield of barley due to dry growing conditions in subarctic Alaska have been reported by several researchers (Knight 1994, Sharratt 1994, Cochran and Schlentner 1995).

The patterns in dry matter accumulation by plants at low or zero grasshopper density show striking differences between years. The data suggest that, in 2003, yield may have been sink limited. Fewer seed primordia seem to have been initiated, or fewer spiklets were fertile, during the 2003 early season drought. Consequently, there were fewer seeds per head. With the favorable growing conditions later in the season, these seeds grew larger. Even though the early season drought may have limited growth of vegetative struc-
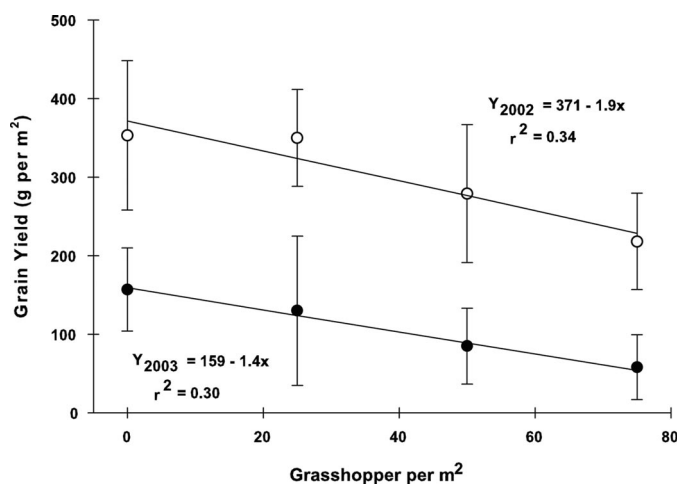

Fig. 3. Regression of grain yield (grams per square meter) on numbers of grasshoppers in 2002 (open circles) and 2003 (filled circles). Each point represents the mean of eight observations. Error bars represent 1 SD.
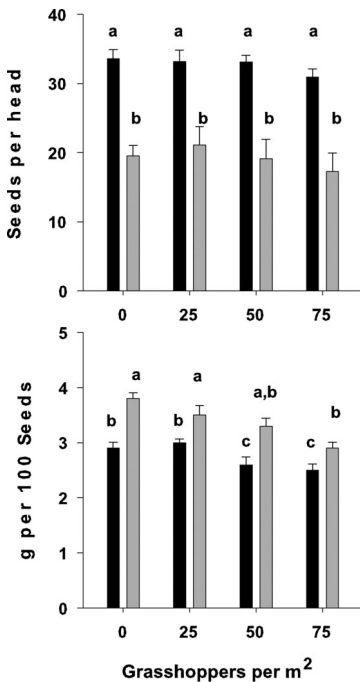
Fig. 4. Number of seeds per head and seed weight in relation to grasshopper density in 2002 (black bars) and 2003 (gray bars). Means with the same letter do not differ significantly at $P < 0.05$, LSD.

tures, thereby reducing the photosynthetic capacity of the plants throughout the season (Gardner et al. 1985), apparently the plants were able to largely meet the demand for assimilates during grain fill with current photosynthesis because of the relatively small sink. The low percentage loss of dry matter from just after anthesis (harvest 2) to maturity (harvest 3) in the low grasshopper treatments and controls in 2003 (Fig. 1) is consistent with the hypothesis of sink limitation, i.e., the grain sink was not large enough to draw significant quantities of translocated carbohydrates. Also, the lower harvest index in 2003 is consistent with sink limitation. With fewer seeds per head to absorb translocated assimilates, the proportion of aboveground dry matter represented in the grain would be limited. In 2002, the loss of nongrain dry matter from harvest two to harvest three was much greater, proportionally and in absolute terms, than in 2003, suggesting that substantial translocation of nonstructural carbohydrates occurred during grain filling. Also, the dry weight of the grain in 2002 was much greater than the gain in total dry matter from anthesis to maturity, an observation consistent with mobilization and translocation of carbohydrates.

In contrast, grasshoppers affected yield through source limitation by removal of photosynthetic tissue. Grasshoppers reduced weight of the seeds, but not numbers of seed, in both years (Fig. 3). This is in agreement with other studies of defoliation in small grains, where yield reduction is primarily due to smaller grain size, rather than fewer grains (Ryle and

Powell 1975, Olfert and Mukerji 1983, Aggarwal et al. 1990). Grasshoppers had no effect on harvest index. Chauhan and Gopal (1983) reported that defoliation at any stage of barley growth affects both the growth and yield to some extent, but the harvest index remains almost unaffected. Early season damage by the grasshoppers apparently was not enough to reduce the number of seeds.

Weed pressure was low in both years. One explanation for the lack of weed pressure is that the plots were located on land only recently recleared from forest. Conn and DeLapp (1983) found that the number of years in cultivation was a better predictor of the amount of nonnative weed vegetation in agricultural fields in Alaska than any other soil or management variable measured in their study. They reported that weedy vegetation in fields that had been cultivated for >2 yr became dominated by nonnative weed species such as common lambsquarters, common chickweed, *Stellaria media* (L.) Cyrillo; quackgrass, *Agropyron repens* (L.) Beauv.; and foxtail barley, *Hordeum jubatum* L. In addition, barley is known to be very competitive with weeds, requiring high densities of weeds to reduce yields (Conn and Thomas 1987, Lutman et al. 1994, Christensen 1995, Fischer et al. 2000, Walker et al. 2001). In Alaska, Conn and Thomas (1987) reported a 36% reduction in barley yield in Alaska with 1,300 common lambsquarters seedlings per m^2, much higher numbers than were encountered in the current study.

The regressions of yield on grasshopper density may be used to provide a preliminary estimate of the economic injury level, for situations where defoliation begins in mid-season and continues up to harvest. The relationship between grasshopper density and yield, averaged over weed treatment, was found to be highly significant and linear in both the 2002 ($P = 0.0005$) and 2003 ($P = 0.0013$) growing seasons (Fig. 3). The fitted linear relationships suggest an average yield loss of ≈1.6 g/m^2 (or 16 kg/ha) for every grasshopper per square meter (Fig. 1). The 8-yr average price of barley grain to the producer in Alaska is ≈$0.156/kg (Benz et al. 2002). The costs to control grasshoppers in Alaska are estimated to be ≈$12.00/ha for the chemical and application costs are estimated at $20.00/ha (Doane's Agricultural Report 2003). Thus, a rough estimate of an economic threshold is ≈13 grasshoppers per m^2. This is within the range of grasshopper densities, within a variety crops, that is considered to probably justify treatment in Nebraska (Hein and Campbell 2004).

Delayed senescence is the most widely and commonly reported plant response to defoliation (Higley 1992, Haile et al. 1998). Under longer growing seasons, yield reductions may be minimal due to delayed senescence; and plants may experience improved light, water, and nutrient status after defoliation, compared with undefoliated plants (Higley 1992, Haile et al. 1998), which could compensate for the reduced leaf area. However, under short growing seasons, such as in Alaska, plants may not have enough time to compensate for insect injury. We noted some evidence of

delayed senescence in this study, but we did not attempt to quantify it. In this study, yield reduction was primarily through reduced seed weight and head clipping. Because head clipping has the potential to result in large crop losses, the factors that lead to head clipping need further research.

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